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Adaptation to climate in five eastern North America broadleaf deciduous species: Growth clines and evidence of the growth-cold tolerance trade-off

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ABSTRACT

Clines in genetic variation along climate gradients documented for many species in temperate and boreal forests illustrate adaptation of forest tree populations to climate. Adaptation tends to involve balancing selection between high growth rates and stress resistance: a trade-off in resource allocation between stress tolerance and competitive ability that determines fundamental life history strategies. The growth-cold tolerance trade-off, in particular, has been well documented for many conifers but evidence in broadleaf deciduous species is scarce. Using populations' mean total tree height and provenance climate from range-wide provenance tests established in the USA between 1960 and 1975, we evaluate and model growth clines along climatic gradients and assess evidence of the growth rate-cold tolerance trade-off in five eastern North America broadleaf deciduous species: *Acer rubrum* (red maple), *Betula alleghaniensis* (yellow birch), *Juglans nigra* (black walnut), *Prunus serotina* (black cherry), and *Quercus rubra* (northern red oak). Number of populations and provenance tests in this study varies by species, ranging from 31 to70 and 4 to 8, respectively. For each species, observations were separated into two groups, those where the population was moved to a test site climate milder than at its origin, and those where the population was moved to a colder test site climate. Clines of growth potential along climate gradients were evaluated using the group of observations in which the populations had been transferred to a milder test climate, while cold-limited responses were evaluated using the observations in the group of populations moved to colder test climate. Results showed steep clines in association with temperature variables for black walnut and black cherry and less pronounced clines for red maple. Population differentiation in northern red oak and yellow birch was weak. Growth potential clines had slopes opposite to the cold-limited growth responses, providing strong evidence for the growth-cold tolerance trade-off in broadleaf deciduous species. The results show that genetic growth responses to climate will differ considerably among species and thereby demand different management strategies to mitigate climate change impacts.

1. Introduction

Adaptation to climate in species of temperate and boreal forests involves a trade-off between selection for high growth rates and for stress resistance (see Morgenstern, 1996). Low-stress, high-resource environments tend to favor fast-growing populations, whereas high-stress, low-resource environments favor populations that are cold or drought hardy (Endler, 1977; Rehfeldt, 1984). As a result, the intraspecific outcome of this resource allocation trade-off involving stress tolerance and competitive ability becomes a fundamental life history strategy (Grime, 1979).

In forest trees, the growth-cold tolerance trade-off has been well documented for many species, mostly conifers. It develops from the close timing of annual growth events with the length of the frost-free period which produces a negative relationship between the amount of growth and cold hardiness (Rehfeldt, 1991; Howe et al., 2003; Aitken and Bemmels, 2016). Populations adapted to cold climates with short growing seasons tend to be more cold tolerant and slower growing than those adapted to warm or mild climates, even when grown in benign climates (e.g. Rehfeldt, 1984; Rehfeldt et al., 2004). This variation is clinal, that is, differences between populations change gradually along the environmental gradient (Morgenstern, 1996), but clines involving growth are of slope opposite to those of cold hardiness, affirming that selection for high competitive ability occurs within the boundaries of the cold hardiness requirement of the site (Rehfeldt et al., 2004).

Clines are revealed when genetic variation in fitness-related traits are associated with climatic gradients. The traits ordinarily are evaluated in common gardens where natural populations are grown under

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the same environment and cultivation conditions (Campbell and Sorensen, 1978; Rehfeldt, 1984; Davis et al., 2005; Etterson et al., 2016). These common garden studies, known as provenance tests in forestry, have been used extensively in forest trees to describe patterns of genetic variation, to predict provenance performance based on populations' climate of origin (Langlet, 1971; Campbell, 1974; Rehfeldt, 1984) and, more recently, to understand species and populations' responses to changes in climate (Matyas, 1994; Carter, 1996; Rehfeldt et al., 1999; Wang et al., 2006, 2010; Leites et al., 2012; Rehfeldt et al., 2018). Provenance test results have shown consistent associations between fitness-related traits and climate variables, mainly temperature, providing strong evidence for the molding of opposing clines of growth and cold tolerance by natural selection (reviewed by Howe et al., 2003).

While the climatic clines generally are well described for conifers (reviewed by Aitken and Bemmels, 2016), it is unclear whether knowledge gleaned from conifers is applicable to the broadleaf deciduous forests of eastern North America. For these forests, numerous range-wide provenance tests were conducted for commercially important species between 1960 and 1980, that is, before climate data became readily available. Most tests detected genetic differentiation of populations; some uncovered geographic clines arranged along latitudinal gradients (e.g. Bey, 1973, 1979, 1980; Clausen, 1975; Kriebel et al., 1976; Little et al., 1974; Schmitt and Carter, 1987); but few documented climatic clines (e.g. Townsend, 1977; Steiner, 1979; Patil and Land, 1987).

Our study is aimed at the gap in knowledge between gymnosperms and angiosperms. We use growth measurements in old provenance tests to evaluate and model climatic clines, focusing on the growth potential-cold tolerance trade-off in five prominent broadleaf deciduous species: *Acer rubrum* (red maple), *Betula alleghaniensis* (yellow birch), *Juglans nigra* (black walnut), *Prunus serotina* (black cherry), and *Quercus rubra* (northern red oak). We pose the following questions:

1) Is there evidence of genetic differentiation along climate gradients for these species?
2) What are the climate variables driving that differentiation?
3) How much of the genetic variation among populations is due to adaptation to climate?
4) Is there evidence of a growth-cold tolerance trade-off in these five species?

Following Rehfeldt et al. (1999), we use the term provenance to refer to the geographic location where seed was collected and the term population to refer to the individuals at that location and their natural, wind-pollinated offspring. We use the term cold tolerance to refer to adaptation to cold environments, not necessarily limited to tolerance of cold temperatures. Analyses are made on tree height, widely accepted as a proxy for fitness (e.g. Aitken and Bemmels, 2016).

2. Methods

2.1. Data

Published and unpublished total tree height measurements from range-wide provenance tests established in the USA between 1960 and 1975 were digitized for the five species of interest. Data sources for each species are listed in the supporting information, S1. Provenance tests of these species were established on 4 to 8 test sites with 34–70 populations (Table 1). Each provenance test comprised five or more blocks, except in two tests that had either two or three blocks. Populations were randomly assigned to plots within blocks; plots were either square or single rows and contained 4–16 trees. For each species, a subset of the populations was planted on all test sites, but the number of populations in the subset varied by species, with black walnut having populations planted in more than one site but no population planted in all test sites. For our study, only population means for each test site were analyzed, as no block-level information was available. Climate normals for the period 1961–1990 for all populations and test sites were obtained from Rehfeldt's climate surfaces for North America (Rehfeldt, 2006, data available at: http://charcoal.cnre.vt.edu/climate). This normalization period is used because it best represents the period when the generation of trees under study was established. A summary of the data and the distribution of populations and tests within the geographic range of each species are presented in Table 1 and Fig. 1.

Table 1
Number of tests and populations evaluated, population mean and standard deviation (S) of total tree height across populations and test sites by species.

Species	No of tests	No. of populations	Years in plantation	Mean height (S), cm
Black cherry	4	34	10	345.3 (141.5)
Black walnut	8	70	10	498.3 (148.6)
Northern red oak	6	31	11-13	470.1 (127.9)
Red maple	5	51	7	260.9 (61.3)
Yellow birch	4	55	5	241.7 (54.4)

Although we screened a set of temperature and precipitation variables, we focus on temperature variables because (a) clinal patterns of genetic variation have been shown to be strongest along temperature gradients (see review by Aitken and Bemmels, 2016), and (b) previous work with these broadleaf deciduous species found clines in association with latitude (e.g. Bey, 1973, 1979, 1980; Clausen, 1975; Kriebel et al., 1976; Little et al., 1974; Schmitt and Carter, 1987)), which is most strongly correlated with temperature within this region. We concentrate in particular on mean annual temperature (MAT) and growing degree days above 5 °C (DD5), both variables reflecting the mildness of the climate; mean temperature of the coldest month (MTCM), a variable reflecting the harshness of the winter; Julian date at which the growing degree days above 5 C reach 100 (D100), a variable reflecting the spring warmth (lower values indicate warmer spring); and mean temperature of the warmest month (MTWM) and mean maximum temperature of the warmest month (MMAX) to reflect the warmth of summer. The precipitation related variables we consider describe precipitation regimes (April-September precipitation, GSP) and the balance between temperature and precipitation (SDI, the ratio of degree-days > 5 °C accumulated between the last freeze of spring and the first freeze of autumn to GSP).

Supporting information S2 presents MAT and mean annual precipitation (MAP) ranges (climate range hereafter) of each species and for the populations and test sites represented for the species. In all cases, the populations' climate range for both MAT and MAP extends beyond the species interquartile range, showing, therefore, that the populations tested provide a solid representation of the climate variability within the species' distribution. The narrow climate range of the test sites, centered generally within the species climatic range, is characteristic of these provenance tests. For black walnut, however, the climatic range of the test sites overlaps almost completely the species interquartile range for both climate variables.

2.2. Analysis

In order to evaluate growth clines along climate gradients, populations must be tested in environments that allow innate growth capabilities to be expressed (Rehfeldt, 1984). In this study, we made the assumption that innate growth potential is most accurately expressed in test climates that are at least as mild as provenance climates (i.e. warmer), and we will use the term "growth potential clines" to refer to population variation expressed under these circumstances. Similarly, we assumed that cold tolerance is best expressed in test climates that are colder than provenance climates, and we will use the term "cold-limited responses" to refer to population variation expressed under this

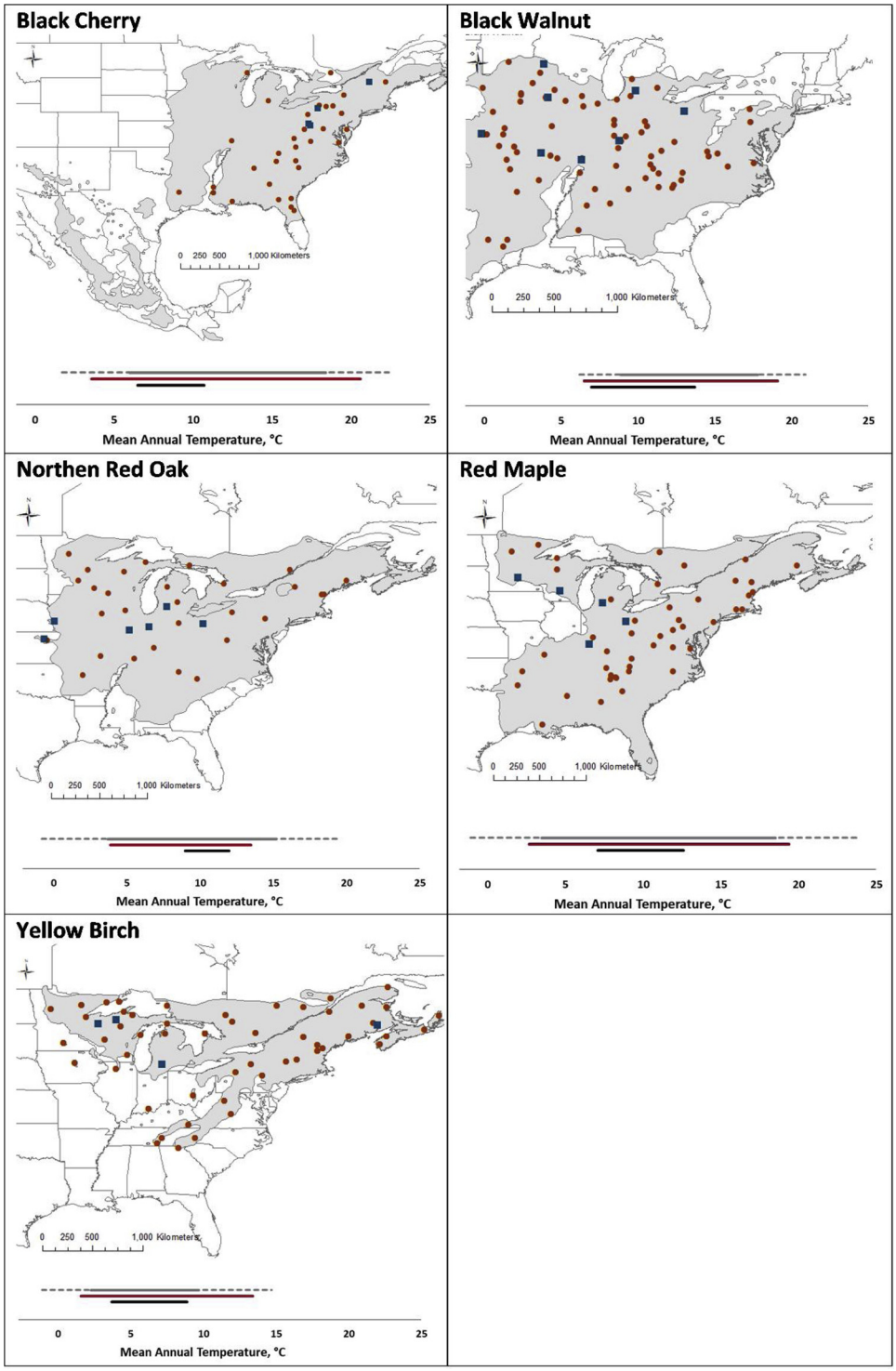
Black Cherry
0 250 500 1,000 Kilometers
0 5 10 15 20 25
Mean Annual Temperature, °C
Black Walnut
0 250 500 1,000 Kilometers
0 5 10 15 20 25
Mean Annual Temperature, °C
Northen Red Oak
0 250 500 1,000 Kilometers
0 5 10 15 20 25
Mean Annual Temperature, °C
Red Maple
0 250 500 1,000 Kilometers
0 5 10 15 20 25
Mean Annual Temperature, °C
Yellow Birch
0 250 500 1,000 Kilometers
0 5 10 15 20 25
Mean Annual Temperature, °C

Fig. 1. Species geographic range (Little 1976) with populations (red circles) and tests (black squares) geographic locations. The graphics beneath the maps show ranges for the mean annual temperature where the species is present (gray line with 0–10 percentile and 90–100 percentile dashed and 10–90 percentile solid, Thompson et al., 2015), for the populations in the sample (red line) and for the test sites (black line). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

set of provenance-test site combinations. To evaluate both types of clines for the five species under consideration, observations within populations were separated into two groups: a) those "moved to milder sites" (growth potential clines), and b) those "moved to colder sites" (cold-limited responses). For this we calculated the climatic transfer distance, defined as the climate at the test site minus the provenance climate (Rehfeldt et al., 1999), for all variables of interest. A negative MAT transfer distance, for example, indicates the population was moved to a colder site and a positive indicates translocation to a warmer site. We used transfer distance zero as the separation between groups and included observations with transfer distance zero in the "moved to milder sites" group. For analyses using precipitation variables, populations were allocated to groups based on transfers to wetter or drier climates. As an aid for interpreting our results, note that many

Table 2
Slope estimates (Equation 1) for growth potential cline (GP, moved to milder group) and cold-limited response (CLR, moved to colder) models with their respective 95% bootstrapped confidence interval in parenthesis. Only slopes statistically significant are reported.

Species		MAT	DD5	MTCM	D100	MTWM	MMax
Black cherry	GP	23.41 (10.8,36.6)	0.163 (0.07,0.26)	13.3(5.04,21.58)	ns	50.30 (30.2,69.9)	33.71 (17.63,52.1)
	CLR	−11.12 (-17.3,-5.4)	−0.051(0.072,-0.028)	−6.89(-11.5,-2.4)	1.33(0.63, 2.0)	−20.45(-31.9,-8.5)	−23.73(-36.5,-11.4)
Black walnut	GP	18.64 (7.6, 29.5)	0.108 (0.04,0.16)	7.46 (0.88,13.5)	−3.05 (-5.2,-1.2)	ns	ns
	CLR	−14.78 (-21.5, -8)	−0.044 (-0.07,-0.02)	−9.27 (-13.5,-5.1)	1.57 (0.81,2.3)	ns	ns
Northern red oak	GP	ns	ns	ns	ns	9.38 (2.9,15.8)	13.35 (7.5,19.8)
	CLR	ns	ns	ns	ns	ns	ns
Red maple	GP	6.50 (2.3, 10.6)	ns	3.94 (1.1,6.7)	−1.58 (-2.4,-0.75)	ns	ns
	CLR	−9.10 (-13.8,-4.1)	−0.037 (-0.06,-0.01)	−7.10 (-10.1,-4.2)	1.15 (0.53,1.8)	−15.77 (-28.1,-2.7)	−17.44 (-30.3,-3.5)
Yellow birch	GP	6.44 (1.5, 11.6)	ns	4.22(1.0,7.7)	ns	ns	ns
	CLR	ns	ns	ns	0.567 (0.02-1.2)	ns	ns

populations were represented in both groupings. For instance, when using MAT transfer distance, the percent of populations shared by both groups ranged between 53% for yellow birch to 9.7% for red maple.

We address questions 1 and 2 in the following way. For each species and climate variable, we develop univariate mixed-effects linear models (lme4 package in R, Bates et al., 2015) using a) the observations from the "move to warmer sites" group, and b) using the observations from the "moved to colder sites" group. These models predict population mean total tree height as a function of the population's provenance climate (fixed effect) and include test site and population as random effects affecting the intercept (Eq. (1)). For some of the models, there were only one or two observations per population and thus the population random effect was not included. For northern red oak, age was included in the model as a fixed effect (see Table 1). We evaluate the statistical significance of the slope for the provenance climate variable by constructing bootstrapped 95% confidence intervals for the slope estimate using 1000 simulations. We interpret a slope significantly different from zero as evidence of a genetic growth cline along the evaluated provenance climate variable.

$$Ht_{jk} = \mu + \tau_j + \varphi_k + \beta_1 hc_j + \varepsilon_{jk} \quad (1)$$

Ht_{jk} is the mean total tree height of population j in test k, μ is the mean or intercept, τ is the population random effect, φ is the test site random effect, β_1 is the slope, hc is the provenance climate fixed effect and epsilon is the error.

To address question 3, we focused only on the models (Eq. (1)) for which the climate variables had a slope statistically different from zero ($\alpha = 0.05$). Test site is a major effect in the mean total tree height for each of the species. The test site effect not only includes environmental differences such as climate and soil productivity, but also different management regimes such as weeding and unique events such as rodent attacks or disease episodes that can obscure the detection of clines by inflating to genotype by environment interactions (e.g. Campbell and Sorensen, 1978). Correcting observations for test site effects thereby allows us to estimate the proportion of population variance that is explained by the clines. Therefore, average test site effects were removed from each observation by subtracting the best linear unbiased predictor (BLUP) of the test site random effect for the corresponding model from such test's observations (corrected height hereafter). The variation among the corrected height can then be attributed to variation among and within populations as well as experimental error not accounted for by the test site effect. We then calculated the proportion of variation accounted for by the provenance climate by fitting a simple linear model of the corrected height against the predictions (fixed effects) from Eq. (1). To compare slopes among species with different mean tree height we standardized the corrected height by dividing it by the mean total tree height of the observations used to fit the model.

To address question 4, we compare the slope of "moved to milder" and "move to colder" regression models for each provenance climate variable producing significant slopes. Slopes of opposite signs for each pair of models would suggest a growth-cold tolerance trade-off in each species.

The same set of analyses was performed using the precipitation variables. The results, however, showed genetic effects to be weak for two clines in red maple and black walnut and one cline for black cherry but otherwise nonexistent. Where detected, the clines accounted for little of the variation among populations (range 2.7%–11%). The remainder of this paper focuses, therefore, on temperature-related clines. All analyses were performed in the statistical computing environment R (v.3.3.2, R Core Team, 2016).

3. Results

Clines in growth potential were detected for at least one climate variable in all species while clines in cold-limited responses were detected for all species except northern red oak (Tables 2 and 3). For black cherry and red maple, both cline types were detected for all provenance climate variables evaluated, but for black walnut, both types were detected for four of the six provenance climate variables. Clines in growth potential for black walnut, black cherry and red maple accounted for as much as 44%, 41%, and 29% of the populations' corrected height variance, respectively, while cold-limited growth clines accounted for

Table 3
Proportion of the variation in corrected height explained by the provenance climate variable (fixed effects predictions, Equation 1) for the growth potential clines (GPC) and the cold-limited responses (CLR), and number of observations (n) for each model.

Species		MAT	DD5	MTCM	D100	MTWM	MMax
Black cherry	GPC	39% (n = 37)	32% (n = 40)	41% (= 35)	–	37% (n = 45)	24% (n = 57)
	CLR	38% (n = 67)	27% (n = 64)	19% (n = 69)	27%(n = 68)	27% (n = 59)	28% (n = 57)
Black walnut	GPC	44% (n = 40)	38% (n = 45)	35% (n = 30)	37% (n = 34)	–	–
	CLR	22% (n = 115)	13% (n = 111)	20% (n = 125)	17%(n = 121)	–	–
Northern red oak	GPC	–	–	–	–	12% (n = 119)	18% (n = 120)
	CLR	–	–	–	–	–	–
Red maple	GPC	23% (n = 92)	–	22% (n = 78)	29% (n = 96)	–	–
	CLR	24% (n = 59)	21% (n = 50)	36% (n = 73)	23% (n = 55)	17% (n = 40)	16% (n = 40)
Yellow birch	GPC	11% (n = 84)	–	12% (n = 77)	–	–	–
	CLR	–	–	–	7% (n = 79)	–	–

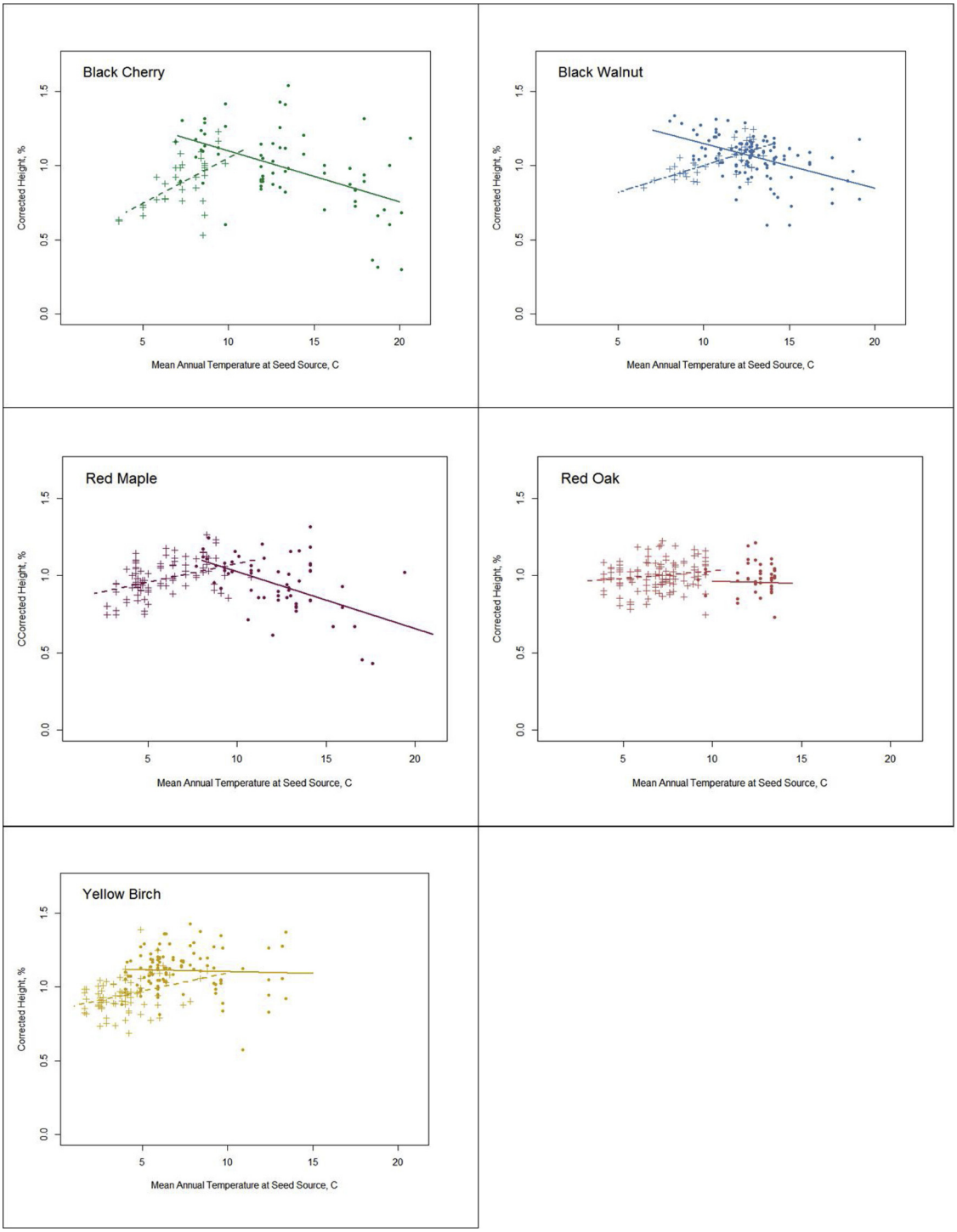

Fig. 2. Growth clines along MAT and site-corrected population mean tree height observations expressed as percent of the mean tree height of the fit dataset for the five species: growth potential clines and "moved to milder sites" observations (dashed line, cross symbol), and cold-limited responses with the "moved to colder sites" observations (solid line and circle symbol).

as much as 22%, 38%, and 36% (Table 3). For northern red oak and yellow birch, few clines were detected (Table 2), and the percentage of the phenotypic variation in population corrected height was low, averaging only 12% (Table 3).

To facilitate comparison, models illustrating the growth potential and cold-limited growth clines for MAT are presented (Fig. 2) for all species using the corrected height as a percent of the mean tree height of all observations used to fit the model. Note that for northern red oak and yellow birch, the slope of at least one of the MAT models was not significantly different from zero at $\alpha = 0.05$ (Table 3) but we have nonetheless presented them in the figure. Judging the relative steepness of these clinal responses among species should be done by considering together the slope of both cline types (Table 2) and the percent of variation in population mean corrected height accounted for by the provenance climate (Table 3). Doing so leads to the conclusion that black cherry and black walnut have the steepest temperature-related clines; that for red maple is intermediate; and those for yellow birch and northern red oak are weak.

Of the provenance climate variables tested, MAT and MTCM were related to growth clines in slightly more cases than the other variables (Table 2), while variables associated with summer warmth were related to growth in only a few cases. The percent of the variation explained by provenance climate ranged from 7 to 44% depending on the species, climate variable, and model type. None of the climate variables we evaluated stands out from the others as explaining more variation in growth across the five species, although the average percent of explained variation across species is highest for MAT. On average, both growth potential clines and cold-limited response cline models explained similar percent of variation (28% and 22% respectively).

For all species, slopes of the growth potential cline models had opposite sign to the slopes of the cold-limited response models for each given provenance climate variable. The opposite signs for these coefficients provide strong evidence of the growth-cold tolerance trade-off: populations originating in warmer areas had higher growth potential and were more affected when moved to the colder sites than populations from colder areas. For those species with significant clines for both growth potential and cold-limited response for not only the same climate variable but for multiple climate variables, we calculated correlations between the pair of slopes for both models using the same climate variable (Fig. 3). The Pearson correlation for all three species ranged from -0.90 to -0.99. This provides additional evidence of the growth-cold hardiness trade-off in these species.

4. Discussion

In this new analysis of provenance test data, we verify for five broadleaf deciduous species genetic principles documented for several conifers (Howe et al., 2003; Rehfeldt et al., 2004, 2018): innate differences in population mean tree height occur along climate gradients in all species evaluated and provide evidence of a growth-cold tolerance trade-off. For all five species we evaluated, the warmer the provenance climate, the higher the population mean tree height when grown in mild environments, and the lower the population mean tree height when grown in cold environments. This reflects how populations of temperate forest tree species have adapted their annual developmental cycle to fit the frost free period. The suite of traits that determine the length of the annual growth cycle, i.e. time of bud burst, period of shoot elongation, time of bud set, period of leaf and diameter growth, and duration of bud development, negatively correlate with cold tolerance as late growth initiation and early growth cessation help the plant avoid late spring and early autumn frosts respectively, and growth cessation is required before cold acclimation can begin (Rehfeldt, 1984; Howe et al., 2003). This correlation confers either high growth potential in mild environments or high cold tolerance in harsh environment. Southern or low elevation provenances have longer growing seasons and grow taller but are more susceptible to late spring and early autumn frosts. Northern or high elevation provenances stop growth earlier than southern populations and are short but cold hardy (Rehfeldt, 1990; Morgenstern, 1996).

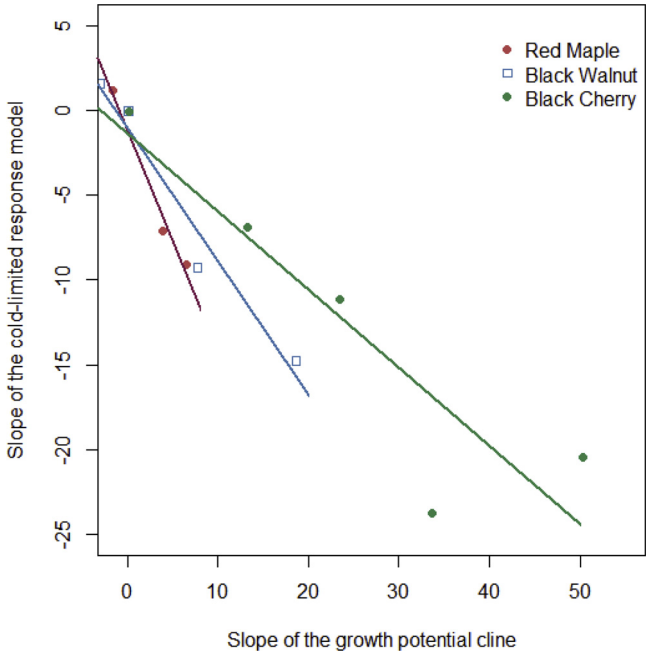

Fig. 3. Relationship by species between the slopes of the growth potential cline and the cold-limited cline for provenance climate variables for which both models were statistically significant ($\alpha = 0.05$). Black cherry $r^2 = 0.82$, Black walnut $r^2 = 0.96$, Red maple $r^2 = 0.98$.

When interpreting provenance test results, it should be noted that the dispersion of populations tested, and the location of test sites can affect the detection of clines and, therefore, their steepness. For our analyses, test sites typically were located well within the species climatic range (Fig. 1). The central location of these test sites constrained the diversity of populations making up the “moved to milder sites” and “moved to colder sites” groups (Fig. 2). The regressions, therefore, were deprived of extreme data points and, therefore, may have underestimated the steepness of either cline, particularly if the clines were nonlinear. Consequently, where clines were detected, evidence for differentiation is strong, but the true clines are likely to be more pronounced than estimated. Where not detected, clines are either weak or non-existent, or constraints of the data set limited the power of the statistical tests to detect them.

For the species evaluated, clines in black cherry tended to be the steepest, that is, characterized by slopes of the largest magnitude and provenance climate explained a large proportion of the variation in population mean tree height (Fig. 2). Clines for black walnut and red maple were less steep than those for black cherry, and clines for yellow birch and northern red oak were weak. Species with steeper clines reflect the role of natural selection in dealing with high spatial climate variability; populations are closely adapted to different environmental segments (Rehfeldt, 1984). On the other hand, species with relatively flat clines, i.e., greater homeostasis in response to temperature gradients, are exhibiting either a high degree of physiological adjustment or a low degree of growth optimization in response to natural selection. This strategy may be more effective where temporal environmental variability is high or unpredictable (Rehfeldt, 1984). Below we provide a brief discussion of this study results within the context of previous work for each of the species.

4.1. Black cherry

Of all species evaluated here, black cherry presented the steepest clines which were evident for all provenance climate variables evaluated. Early studies in geographic variation of this species indicate the presence of population differences in phenology (leaf and flower development in spring, Genys and Cech, 1974), survival (Carter et al., 1983), and growth rates (diameter and height growth, Patil and Land, 1987). Geographic variation is so pronounced in this species that McVaugh (1951) recognized five subspecific taxonomic categories (cited by Carter et al., 1983). The steepness of the clines we detected would be consistent with the genetic variation previously described in this species.

4.2. Black walnut

We detected strong clines in growth potential in black walnut, with the variation in corrected height explained by seed source MAT being the highest of any of the species evaluated (44%). Previous studies also indicate differences in growth related to population origin (Bey, 1973, 1979), attributing the differences to the long growing seasons for

southern populations (Wright and Lemmien, 1972). In our study, the black walnut cold-limited responses were less steep than those for black cherry and red maple. This seems to confirm early studies documenting differences in cold tolerance within the species but also describing "a great deal of inherent cold hardiness in black walnut" (Schmitt and Carter, 1987; Brensan et al., 1994). Old seed collection guidelines for this species advocated using seed from sources as far as 200 miles south of the plantation site to be safe in terms of cold hardiness but yet capture improved growth potential (Little et al., 1974; Deneke et al., 1980).

4.3. Northern red oak

Growth potential clines along MTWM and MMAX were the only clines detected for this species. Kriebel et al. (1976) documented a north-to-south trend on autumn coloration. Because coloration signals the start of dormancy and is conditioned by the length of the growing season, our results are consistent in that high MTWM and MMAX correspond to long growing seasons. The clines we detected, however, were weak, accounting for < 20% of the variance in population corrected height. Two conclusions can be drawn from this: either genetic differentiation is weak within this species or real clines remain undetected by our analysis. Indeed, the lack of cold-limited responses could be explained by a lack of southern populations tested (Kreibel et al., 1976). Yet, our analysis detected only weak clines in growth potential that accounted for a small proportion of the variation in corrected height. The results together support a conclusion of weak intra-specific genetic differentiation. Previous studies have found genetic differences in phenotypic variation but indicate that such variation may be more complex than for other species (e.g. Kreibel et al., 1976; Schlarbaum and Bagley, 1981). Regionally, within-population variation may represent 88% (age 6) to 95% (age 3) of total additive genetic variance in juvenile growth rate (Steiner et al., 1996, 2000). Although additional studies may be necessary for a better assessment of this species, our analyses suggest clines of low trajectory and, therefore, the importance of phenotypic plasticity in accommodating environmental variation.

4.4. Red maple

Of all species tested, red maple showed the strongest cold-limited response driven apparently by MTCM. Previous studies, moreover, documented genetic variation in several traits related to cold hardiness in this species; a positive correlation between timing and intensity of fall coloration with latitude; a negative correlation between winter injury and latitude or elevation; and slower growth rates stemming from winter damage in southern populations growing on cold sites (Townsend, 1977, 1979, 1982). Our results are in agreement, thus suggesting differentiation in cold tolerance to be important in this species.

4.5. Yellow birch

Clines detected for this species were few and accounted for little variation in corrected height. Here again there are two plausible conclusions: no genetic differentiation within the species or not enough statistical power. In favor of the former, the range of populations tested is a good representation of the species range (Fig. 1). Early analyses of this study also detected no clear geographic patterns of variation in mean tree height for this species either (Clausen, 1975). In the present study, we found clinal variation in population mean tree height along MAT, MTCM, and D100, but they did not explain large part of the phenotypic variation.

4.6. Implications for understanding species responses to a warming climate

Describing range-wide patterns of intra-specific genetic variability is critical for understanding climate change effects on forest tree species, improving projections of species range shifts, and conserving genetic diversity. A warming climate would result in more disruption per unit of temperature change for species composed of locally adapted populations, i.e. species with steep genetic clines driven by climate, than for species with weaker locally-differentiated climatic adaptations. Populations are not only adapted to a segment of the environmental niche inhabited by the species, but may also inhabit suboptimal climates, that is, their ecological optimum differs from the physiological optimum (e.g. Namkoong, 1969; Rehfeldt et al., 2018). For many species, the difference between the ecological and physiological optimum is wider for cold adapted populations and, for a given magnitude of warming, populations adapted to colder areas likely will increase growth before maladaptation is expressed, while populations adapted to warmer areas will be likely to express maladaptations first (see Rehfeldt et al., 2018). Trailing edge populations should be the focus of conservation earlier than populations in the leading edge as they will likely be affected sooner and as well may hold unique genetic diversity (Hampe and Petit, 2005; Jump et al., 2008).

Species distribution models that treat the species as a homogenous unit (e.g. Iverson and Prasad, 1998; Prasad et al., 2007-ongoing) will likely underestimate the magnitude of species-level impacts (Zimmerman et al., 2010; Hällfors et al., 2016). Under a warming climate, even if an area remains suitable for the species, it may not remain suitable for the population inhabiting that area (e.g. Joyce and Rehfeldt, 2013). Recent attempts to incorporate intra-specific variation in species distribution models demonstrate the importance of doing so for species with locally adapted populations (e.g. O'Neill et al., 2008; Benito Garzón et al., 2011; Oney et al., 2013). Our results indicate that studies of range shifts in black cherry, black walnut and red maple would require taking into account intra-specific genetic variation.

4.7. Management implications

Understanding intra-specific genetic variation is important in reforestation. Seed zones and seed transfer guidelines are forestry practices intended to ensure adaptation of planted seedlings. Seed movement must have greater restrictions for species with steep clines than for those with relatively flat clines. Likewise, assisted migration of populations as a management strategy to align genotypes with climate under a warming climate (Pedlar et al., 2012) should differ according to cline steepness and should take into consideration the growth-cold tolerance trade-off. Under assisted migration, warm adapted populations would be transferred to areas where the future climate is predicted to be as warm as the population's provenance climate (e.g. Rehfeldt and Jaquish, 2010; Gray et al., 2011; Rehfeldt et al., 2014). Those transferred populations will have to compete with local populations that are presumably adapted to the current climate but have become mal-adapted as the climate has and continues to change. If the immigrant populations have higher growth rates (adapted to warmer climates) that cannot yet be realized because of cold-limited growth, then survival is compromised by competition with the local population. In eastern North America forests, natural regeneration is the norm but supplemental planting is used to ensure adequate regeneration or to achieve a desire species composition. In these cases, assisted migration of populations can be easily implemented but considerations of cold tolerance and its effects on immigrant populations' competition ability is crucial.

5. Conclusions

We assess genetic differences in growth responses to climate in five eastern North America broadleaf deciduous species and document the

trade-off that develops from balancing selection for population growth rates and cold hardiness that is well known in conifers but heretofore not resolved in deciduous forest trees. Black walnut and black cherry present steep clines along temperature variables, followed by red maple. Northern red oak and yellow birch present weak differentiation. The differences in the steepness of the clines that distinguish these species suggest different evolutionary modes for accommodating the heterogeneous environments that comprise their geographic distributions. The results show that genetic growth responses to climate will differ considerably and different management strategies would be necessary to mitigate climate change impacts in these species.

CRediT authorship contribution statement

Laura P. Leites: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Writing - original draft. **Gerald E. Rehfeldt:** Conceptualization, Methodology, Writing - review & editing. **Kim C. Steiner:** Conceptualization, Writing - review & editing.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ppees.2019.02.002.

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